

## OUTLOOK TO THE FUTURE OF SPONGES

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Evidence from the past and recent discoveries provide material for a philosophical review and possible scenarios, for the future of sponges, their essential characters, their evolutionary potential and direction, and their survival. Their short and long term futures appear secure. Species are capable of coping with the outcomes of human impacts on the oceans (survival in highly polluted, warmer waters, in dark and oligotrophic conditions), whereas increased sedimentation is a potential problem to the deep-sea species. Recent species have an ancient, simple 'bauplan' more-or-less unchanged since Precambrian times and are capable of simplifying (independently losing the essential poriferan characters of the aquiferous system and choanocytes), much like the newly discovered Precambrian fossils, to adopt a carnivorous life style. To date, 'complexification' in sponges has been restricted to their considerably complex biochemical constituency and numerous biosynthetic pathways and their ability to develop a canal system, filter-feeding habit and single layer of choanocytes which permit them to attain larger sizes and to have considerable ecological success. But the oldest fossils show that Precambrian sponges did not have such filtering devices and new findings show that carnivorous sponges can certainly live without them. These characters, therefore, are probably not fundamental characteristics of Porifera, which may be better defined by their characteristic cell motility, plasticity of body organisation, absence of tissues and organs and presence of spicules (although the latter optional). □ *Porifera, body plan, carnivory, Precambrian fossils, evolutionary trends, defining characters.*

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The future of sponges, in the context of this review, could be seen from different viewpoints depending on the time scale that is adopted, and whether we look at the question from the human or the sponges' perspective. I could focus on the immediate future of sponge studies: such as emphasising the possible development of molecular tools in reconstructing phylogenies; the expected increase in knowledge of sponge biology; the implications of knowing a complete sponge genome (as predicted by Claude Lévi, this volume); or the impact that machines of the future, successors to our current primitive computers, will have on taxonomy. These concepts have already been considered by Patricia Bergquist (this volume), predicting the next five years. Any prediction over a longer term is not reasonable, because over the next decade techniques are likely to change so spectacularly that the mere extrapolation of existing trends will not provide the insight necessary to make forecasts. We all feel that considerable changes are occurring, and I could predict that molecular taxonomy will demonstrate that Halichondrida are to be merged

with Hadromerida, or that Homoscleromorpha is another phylum, but such predictions cannot be taken seriously or would be based on preliminary results, and that concerns the Present.

This paper, instead, considers the potential evolution of sponges, both in the relatively short term (i.e. during the dramatic changes that humanity has imposed on our planet) and in the far longer term (the future of life on Earth). These predictions are even more uncertain than those concerning the immediate future of sponge research and are matters of philosophy rather than science. I feel more comfortable in this role: there is no risk that I will be disproved in my lifetime. Claude Lévi (this volume) noted that in the early 18th century Dutrochet was wrong when he thought that sponges functioned as an osmotic pump; but who will be there to remember that I was wrong when predicting that sponges would develop a nervous system, or a locomotory apparatus, during the next 200my?

**SHORT TERM.** The relatively short term future of sponges will certainly be modified by humanity. They will have to face disruptions to the

ecological equilibrium caused by the proliferation of our species and activities. We can infer from the rate of extinction over the last two centuries that we are facing a major extinction period of the same order of magnitude as the seven or eight recorded in the fossil record. Sponges have survived these major extinction periods, with up to 80% of marine species known from the fossil record disappearing at the end of Permian. It is therefore likely that they will have a chance of being able to cope with this new threat. We fear a rise in sea-level due to global warming. This is not a problem for sponges. They have seemingly failed in their role, discovered by a French humorist, Alphonse Allais, around 1900, who maintained that sponges were placed in the oceans by Providence to prevent overflowing from all the rivers, but this failure may be turned to their advantage, as more seabed surface will become available for colonisation. A little more seriously, the colonisation or urbanisation of the ocean by mankind, as predicted by some visionary architects, could also turn to the advantage of sponges, which generally prefer solid substrates to soft sediments. These futuristic developments could include submarine cities, with house walls covered by brilliantly coloured sponges, cleaning the water by their filtering activity, with equipment for farming genetically modified species producing molecules of exceptional biological interest.

Many sponges are able to live in polluted areas, so that a scenario of general pollution of the oceans may cause change in species composition but is unlikely to compromise the survival of the phylum. One cause for concern, however, is a global increase in sedimentation rates, which most sponges do not appreciate. This could be a problem for deep-sea sponges impacted by the run-off from intensive land deforestation and erosion, or in the case of careless exploitation of abyssal mineral nodules, a project which is at present discarded but which reappears periodically. Increase in sedimentation is likely to affect first the Hexactinellida, which have a highly efficient but more delicate aquiferous system. A nuclear winter of two or three years would probably decrease sponge diversity, but again without compromising the survival of species that are presently able to live in dark, oligotrophic conditions.

**LONG TERM.** The phylum Porifera thus has a good chance of surviving this new extinction crisis, certainly better than the species causing it — man. After an extinction crisis biodiversity

recovery apparently requires 5-10my (Jablonski, 1994), which is long in our history but very short in the history of life on Earth (which may last up to 5 billion years). What will happen during this time for Porifera? The main question is: will this evolution modify the fundamental body plan, or 'bauplan', of Porifera? This presupposes that we agree on the definition of this fundamental body plan.

The current view of the evolution of metazoans is that the fundamental bauplans which define the various phyla appeared suddenly, that is 5-10my, during a highly imaginative period which has been called the Cambrian explosion. The subsequent evolution of taxa, over approximately 550my, entailed the extinction of many of these types of organisation, whereas a few survivors impressively diversified, but without any fundamental change or creation of any new fundamental types. This pattern of evolution was believed to have occurred mostly by 'complexification' and 'progress', partly because one of nature's most recent products, the 'sumum', is *Homo sapiens*. These views of 'progress' are now strongly challenged, as popularised by Gould (1997). Although it is difficult to be entirely free of this intellectual bias, evolution no longer appears to be directed toward complexification and progress, but alternating between complexification and 'simplification', which thus makes the outcome very difficult to predict.

The phylum Porifera conforms to a very simple body plan, succinctly defined by Bergquist (1978): '... a sedentary, filter-feeding metazoan which utilises a single layer of flagellated cells (choanocytes) to pump a unidirectional water current through its body'. A long accepted view is that this type of organisation, which is the simplest to be found among the successful metazoan survivors, was the first to appear. As a consequence, Porifera is considered as an old phylum, whose evolution has been completed, and whose simple body plan could not complexify like those of other metazoans which developed tissue, organs, guts, eyes, nervous system, etc.

What is true in these assumptions? Their discussion in the knowledge of recent findings on sponge biology could modify the view of the astrologer. Several lines of evidence confirm that sponges are very old metazoans. Biochemical data indicate that although they are true metazoans, several molecules appear as phylogenetically the oldest within the metazoans (review in Müller, 1998). For instance, the time

of divergence of galectin or of the cell-surface RTK (Receptor Tyrosine Kinase) from those of other metazoans has been estimated by Müller from 800–650my. The fossil record, as shown by Françoise Debrenne (this volume), gives increasing evidence that sponges very similar to the modern Demospongiae, Hexactinellida and possibly Calcarca, were already present in the early Cambrian, with spicules and presumably body structures not very different from the Recent fauna (Bengtson et al., 1990; Zhang & Pratt, 1994; Gehling & Rigby, 1996). Moreover, the extraordinarily well preserved fossils from Guizhou in South China (Li et al., 1998) indicate that Demospongiae, and probably other sponges, were already present 580mya. This estimate places the modern sponge bauplan significantly earlier than the Cambrian explosion, which is usually understood to have lasted 5–10my and to have occurred 540–550mya. (Bengtson, 1998; Kerr, 1998). In fact the Cambrian explosion concerned a diversification of the Bilateria phyla more so than the diploblasts such as sponges and cnidarians. Therefore, one conclusion could be that if sponges did not evolve spectacularly during the last 500my, they are also unlikely to evolve so much during the next 5000my — in which case my argument is finished.

Nevertheless, let us consider the poriferan 'bauplan'. As Claude Lévi has already noted (this volume), we have probably over-stressed the canal system and choanocyte in the definition of the Porifera.

The Precambrian Chinese fossils are evidently sponges because their miraculously preserved cells closely resemble those of modern sponges, and because they have spicules. Although spicules are not an indisputable character of sponges, being absent in some Recent Demospongiae, the similarity of the oxaeas in the Chinese fossils with those of the Recent Haplosclerida is striking. In passing, it is worth noting that preliminary molecular taxonomic data indicates the order Haplosclerida to be one of the earlier branchings (Lafay et al., 1992). In contrast with these evident poriferan characters, choanocytes and a complex aquiferous system have not been recognised in these Chinese fossils. This is not due to the processes of fossilisation, as the other cell categories (pinacocytes, porocytes, archaeocytes, sclerocytes), are perfectly recognisable in the fossil material. The individuals are also subspherical, with an unusually small size compared with more recent sponges. Does this mean that these first 'sponges' were devoid of an aquiferous system

and had another mode of life that did not allow them to grow larger than about 750mm? This would throw some doubt on the plesiomorphic character of the aquiferous system (which characterises sponges so clearly among metazoans), and of choanocytes (which is so similar to choanoflagellates). But the present observations deal with a few square centimeters of thin sections, and there are still 57km<sup>2</sup> of phosphatite to explore in the Guizhou deposit in South China.

A second case is the carnivorous mode of life in some Recent sponges. These 'sponges' are devoid of an aquiferous system and choanocytes and develop appendages or filaments covered by hook-like microscleres which trap small crustaceans (Vacelet & Boury-Esnault, 1995). Fortunately they have spicules, so we can recognise that they are sponges, and more specifically sponges closely allied to well known families of Poecilosclerida. Their cytology would be typical of Demospongiae, were it not for the absence of choanocytes. In the absence of a digestive cavity, the digestion of the prey occurs by means of a cellular system which is unique among metazoans, with cells individually migrating toward the prey and digesting it. Intense cell migration and dramatic reshaping of the body occur during the processes of prey capture, engulfment and digestion. These animals thus have a cytology of sponge, with the extreme mobility of all the sponge constituents emphasised by Claude Lévi, but without the conventional diagnostic characters of the phylum Porifera.

This adaptation to carnivory is present in several evolutionary lines of the Poecilosclerida, with chelae microscleres indicative of close affinities with Mycalidae or Esperlopsidae. This adaptation also seems to occur in the family Guitarridae, genus *Euchelipluma*, in which the placocheles are disposed along long appendages with the teeth oriented towards the surface (Vacelet, unpublished observations). A special case is the genus *Chondrocladia*, classified in the Cladorhizidae because of its morphology, but belonging to a different line than *Asbestopuma* and *Cladorhiza* as indicated by its isanorae microscleres, and characterised by inflated spheres which collapse when the sponge is collected (Tendal et al., 1993). From preliminary results, although carnivorous, this genus appears to have retained its choanocyte chambers and an aquiferous system, which is probably used in both filter-feeding and inflating the turgid spheres which trap the prey (Kübler & Barthel, 1999, this volume).

As in the Precambrian Chinese fossils, these animals are clearly 'sponges' that lack choanocytes and an aquiferous system. Contrary to the Chinese fossils, however, this seems to be a relatively recent adaptation which has appeared independently in several evolutionary lines of Poecilosclerida, probably one of the most recent orders in Demospongiae. Based on their spiculation carnivorous taxa are closely allied to normal littoral sponges such as Mycalidae or Guitarridae. The development of carnivory has been described in other deep-sea invertebrates, such as tunicates or gastropods, and appears to be related to the present conditions of the deep sea, which are relatively recent and in any case not older than the Cretaceous. Carnivory in sponges could be older than the Cretaceous, as suggested by *Esperopsis desmophora*, a deep-sea sponge whose morphology suggests carnivory and for which a possible affinity with the Ordovician *Saccospongia* has been suggested (Hooper & Lévi, 1989). However, in any case, carnivory does not appear to be a plesiomorphy of Porifera.

There are therefore two indications that sponges could be permanently devoid of choanocytes and an aquiferous system. In the first case, which is still to be confirmed, it appears as a plesiomorphy. In the second case, it appears as a relatively recent loss in closely related evolutionary lines, under environmental constraints.

This second case is of interest for another reason. Carnivorous sponges have been able to discard the filter feeding system otherwise characteristic of poriferans and to develop a unique organisation. Is this a new bauplan? If yes, then this would be a unique case of an appearance of a new body plan after the Cambrian explosion, and of the development of such a novelty arising from an existing phylum. This scenario would be promising for the future: if sponges succeeded once in such a dramatic change, they may be capable of other changes.

My preference is for another interpretation, already suggested by Claude Lévi (this volume). Our definition of the poriferan body plan is not appropriate. Possession of a canal system, filter-feeding habit and presence of a single layer of choanocytes in fact may not be the fundamental characteristics of sponges. Sponges have the ability to develop these structures that allow them to attain larger sizes and to have considerable ecological success, but the Chinese fossils suggest that the oldest known sponges in the Precambrian did not have such filtering devices,

and the carnivorous sponges also show that they can live without them.

Now the question is: what is the true definition of sponges? Cell motility, plasticity of the organisation, absence of tissues and organs, and presence of spicules (although optional), are good candidates, although it is very difficult to write something simple and not rely too much on characters that are absent. Even so, we must not forget that the development of a unique aquiferous system occurs in more than 99.9% of the species. I will leave that to the future of spongology and future advances on these topics. In this context, an animal such as *Asbestopluma hypogea*, which compensates for the absence of filter system through an increased plasticity (Vacelet, 1998), which is able to live and reproduce in 1/2 litre of sea water with a monthly water change and a monthly feeding with a deep frozen piece of shrimp, without the expensive and sophisticated JAMSTEC (referred to by Patricia Bergquist, this volume), appears to me *the experimental animal for the future*.

Let us now suppose that in the next century we will achieve a definition of the bauplan of Porifera taking these new data into account. If the loss of an aquiferous system during development of carnivory is only a return to square one, then the fundamental organisation of the sponge has not changed so much since Precambrian times. Sponges successfully diversified, but they did not attain a high level of 'complexification' as compared with other metazoan phyla. They were unable to develop a nervous system, motility, etc. in 580my. They still have nearly 10-fold this amount of time before the sun boils the oceans, in approximately 5 billion years. What will happen during this vast expanse of available time? Is greater complexification likely? Two prerequisites are required: they must be capable of complexifying, and they must need to do it.

With evolution now seen as a contingent alternating process between complexification and simplification, sponges will certainly complexify again in the future. What are the possibilities? There are some indications that sponges could already be more complex than previously thought. For example, sponges have only primitive cell junctions, but this seems to be rather for functional reasons than for a lack of genetic potential (Müller, 1982). Indeed, during spiculogenesis in *Calcarea*, which needs tight occlusion of a space between several cells, these sponges could develop septate junctions, which



are absent in normal circumstances (Ledger, 1975). There are several examples in biological evolution where the development of a structure precedes its function; for instance several dinosaurs had feathers before they were able to fly. Carnivorous sponges also provide a good example of this phenomenon. The anisochelate microscleres, isanocorae or placocheles of *Mycale*, *Esperiopsis*, *Guitarra*, that have no evident function in littoral sponges, were most probably developed before carnivory, for which they appeared perfectly suited to the capture of prey with only a small change in orientation. An exercise for the future could be: what is the potential for evolution of the structures, genes, molecules, that we are discovering in sponges without having any precise knowledge of their present function?

Recent developments in biochemistry suggest that the phylum already has many requisites for 'complexification'. We know that sponges have receptors and their ligands homologous to those of other metazoans, suggesting the possibility of developing true tissue (Mehl et al., 1998). Collagen type IV specific to the basal membrane has recently been identified in the Homoscleromorpha (Boute et al., 1996), indicating that a true basal lamina, which is required for the establishment of true tissue and organs, is present in sponges. Neurotransmitters are found in sponges, but they are apparently not engaged presently in cell-communication (Mackie, 1990). Another recent discovery is g-crystallins, a protein of vertebrate eye lens, in *Geodia* (Krasko et al., 1997), which presently has no eye, as far as known. There are many other examples, mostly found in the famous *Geodia cydonium*, and our colleague Werner Müller is adding day after day molecules and genes involved in signal transduction, immunorecognition, neurotransmission, etc. These molecules may suggest potentiality for complexification, although it is more likely that in most cases they are plesiomorphies shared with the other metazoans, which, contrary to sponges, were able to develop and diversify functionality for such precursors. Another interpretation is that the molecule is not a precursor, but a vestige of a more complex stage which evolved towards simplicity with loss of function. This is certainly less general, but is worth keeping in mind for some cases.

Thus, sponges may have some potential for complexification, although it is probably limited. It is not certain, however, that a higher degree of complexity will be necessary for their future success. Two points need to be made here.

Firstly, compare the Cambrian archaeocyathids and the Recent calcarean genus *Clathrina*. The first have a sophisticated solid calcareous skeleton, with an extraordinary complex system of openings in the outer wall, and probably a complex soft tissue system for filter-feeding (Debrenne et al., 1990; Debrenne & Zhuravlev, 1992). They became extinct in the Middle and Upper Cambrian. In contrast, it is difficult to imagine a filter-feeding metazoan simpler than a live *Clathrina*, with its asconoid tube, simple spicules and reduced number of cell types. However, Recent species of *Clathrina* are certainly not archaic survivors of primitive sponges. Their number and diversification, their distribution in highly competitive littoral environments, all indicate that they originate from a relatively recent burst in evolution. So, the complex archaeocyathids were highly successful in the Cambrian, but evolution at present retains the ultrasimple *Clathrina*. During the alternating processes of complexification and simplification, such asconoid sponges have reached the simplest possible stage. They are hitting against the wall of simplicity, as Gould (1997) would say, and it may be predicted that simpler sponges will never occur.

Secondly, conditions in the deep-sea apparently favour carnivory versus filter-feeding. Carnivory usually develops through highly sophisticated devices and behaviour patterns, which need a high degree of complexity. Sponges succeeded in developing this mode of life without a spectacular increase in complexity. Why bother to develop a nervous system, digestive cavity, nematocysts or other weapons when there is the ability to efficiently catch the prey and digest it by other means, as is already done by carnivorous plants or some foraminiferans? So it is not certain that Porifera will really need to complexify while maintaining their success and possibly again diversifying in the ocean of the future.

A last wild thought as a conclusion. Metazoans, including Porifera, are monophyletic. They share the same ancestor. This means that some metazoans may have derived directly from a sponge, which is so difficult to define. Could this happen again? It is easier to imagine such a derivation from a sponge that lacks the specialised anatomy of a filter-feeder, such as the extinct Precambrian Chinese sponges, or the carnivorous sponges, some of which have been captive for three years in my laboratory and may be preparing a new burst in evolution ...

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